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BIOLOGICAL BULLETIN

ECOLOGICAL SUCCESSION.

III. A RECONNAISSANCE OF ITS CAUSES IN PONDS WITH PARTICULAR REFERENCE TO FISH.

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Page

I. Introduction.

In the preceding paper we presented certain facts concerning ponds, together with a statement of succession in the ponds at the head of Lake Michigan, without entering into its causes. Succession in ponds is due to many causes. It is only under the most favorable conditions that we can separate these causes one from another without long and careful investigation. The first attempts of ecologists in this line were considerations of the obvious general facts, such as the accumulation of organic detritus and the increased denseness of vegetation. We can give here a hint at the more specific changes in the ponds and the relations of these to fish. The subject is one for coöperative research. At present some of the workers and the necessary funds are not available, and the ponds are being destroyed rapidly. It is therefore improbable that the study can be carried further. This paper deals with the results of a preliminary investigation of the ponds for the purpose of learning something of the causes of distribution and succession of fish and other organisms in ponds.

II. The Present Character and Content of the Ponds.

The ponds with which we are concerned are shown on the map, p. 131, of the preceding paper of this series.[1] This map is essential to the understanding of the data of the present paper. The ponds here considered are an ecological age series, ecological age being determined by a study of amount of sand bottom, humus, etc., as shown in Table I. below. The physiographic history of the region is in full accord with the facts used in deciding age though in this case physiographic history is not essential to the decision. The pond designated as 1 is ecologically youngest, 14 the oldest, and the others intermediate. The measurements, analyses, and quantitative study were carried out on Pond 1, 5*c* (west section), 7*a*, and 14*b* of the map. Some qualitative records from the other parts of pond 5*c*, from 5*b*, and 14*a*, are included with those of the ponds in which the other work has been done.

[1] See "Ecological Succession," II. Biol. Bull., Aug., 1911, pp. 127–151. These are errors in the pond numbers of this paper which should be corrected.

Page 132, line 13, for "56" read 58.

Page 133, Table I., last line, last column, for "15" read 52.

As we have already stated, the ponds which have been studied especially, are parts of the long sloughs which have been long enough isolated to show their efficiency in supporting the fishes which they now contain. The fishes found in the separated ponds are shown in Table XXI. (p. 17) of the present paper.

With the known habits of fresh-water fishes as a guide, the ponds have been roughly measured and area determined, depth and angle of the slope of sides measured, the character of bottom determined, sketched, and the areas of the different kinds estimated on the basis of the sketches, and the dissolved solids and gases of the waters have been determined by chemists. The plant and animal content of the ponds has been analyzed qualitatively and estimated quantitatively.

These results will be presented under the main heads of: (1) Physical Character, (2) Biological Content.

1. *Physical Character.*—(*a*) Topography. The chief topographic features are shown in Table I.

TABLE I.

SHOWING AREA, DEPTH AND SLOPE OF SIDES OF THE PONDS.

Pond.	Area in Meters.	Greatest Depth in Meters.	Average Depth.	Area of Sides Slope 3°–7°.	Area of Side Slope 20°.
1	3,500	0.6	0.3	Much.	Little.
5*c*	3,500	0.9	0.5	Less.	Much.
7*a*	25,000	0.9	0.5	Very little.	Much.
14*b*	10,000	0.66	0.4	Very little.	Nearly all.

The figures representing depth of water are the results of measurement, with estimation in the case of averages. Areas are results of rough measuring by pacing, counting rails in parallel railroads, etc. While portions studied differ in size, they present considerable uniformity of other features.

(*b*) Character of Bottom. The bottom is composed of pure sand, or sand more or less mixed with or deeply covered by humus. The sand or the humus has a considerable mixture of marl at some points in the younger ponds. Vegetation nearly always covers a pure humus bottom. *Chara* and bulrushes sometimes grow on sand and marl bottoms, but in such cases they are scattered and in the table such areas are included with bare sand, because such sparse vegetation does not interfere with the breeding of fish.

TABLE II.

SHOWING KINDS AND AREAS OF BOTTOMS.

Pond.	Area Sand in Square Meters.	Area Humus in Square Meters.	Depth Humus (Average) in Cm.
1	1,000	2,500	2.5 cm.
5*c*	50	3,450	20.0 cm.
7*a*	Very little.	Nearly all.	21.0 cm.
14*b*	None.	All.	24.0 cm.

It will be noticed that the area of sand is much less in the older ponds and the area of humus much greater, due to accumulation of the latter from the decay of vegetation. The depth of humus does not increase proportionately with age because it becomes more compact with time. With the exception of the first pond, the average depth of humus was obtained by dividing the average depth at the center by two. In the case of pond 1, there are large areas with only two centimeters of humus and two deep places which contain humus of considerable depth; we give only an estimate.

(*c*) The Dissolved Content of the Water. For a preliminary study of the dissolved solids of the water we have had a single analysis of the solids and four analyses of the gases made by chemists. (1) Solids. The small value of single analyses of solids is well known; sanitary analysts have pointed out the dangers arising from conclusions drawn from so little data. However, in this particular case, the value of the results is greater than in the case of single analyses of drinking water, because of the following conditions in and about the ponds.

(*a*) The ponds are without outlet and have no streams emptying into them.

(*b*) During rain they have little inwash because nearly all water must filter into them through sand; in case rain falls in such torrents as to actually run in from the sides, the area of drainage is small, being a strip not more than fifteen meters wide on either side of each pond. The ponds than are comparable to balanced aquaria and any variation of dissolved solids must be due in the main to the effect of organisms, of evaporation, and of renewal from rain.

It should be noted that these analyses were made at the end of

the dry season and just at the close of the probable plankton maximum for the year.

TABLE III.

SALTS IN SOLUTION IN PARTS PER MILLION.

Analysis by Mariner and Hoskins (Chicago, Ill.). The collections were made on October 26, 1909. Wolf Lake contains all the species of fish of all the ponds and is added for comparison.

Pond.	1	5*c*	7*a*	14*b*	Wolf Lake.
Magnesium carbonate	84.6	111.9	38.2	77.1	96.8
Calcium carbonate	54.2	27.9	114.3	83.2	14.7
Calcium sulphate	149.6	146.6		18.5	174.2
Calcium chloride				11.4	9.2
Sodium sulphate	26.6	0.4	45.0		5.7
Sodium chloride	30.3	81.9	16.4	11.3	
Sodium carbonate			7.7		
Iron oxide	3.0	3.0	2.6	3.0	5.8
Silica	6.6	3.4	2.0	3.0	6.0
Total solids including those given in Table XVI	420.0	432.0	258.0	251.0	324.0

The table shows no unusal qualitative features. There is a notable decrease in total solids in the older ponds. This may be due to the fixing of the solids by organisms.

(2) Gases. The gas analyses were made with two facts in view: (*a*) Water may be abnormal in gas content, so as to make it impossible for fish to live (Marsh, '08; Juday and Wagner, '08; Birge and Juday, '11). (*b*) The eggs of all food fishes known to be in the ponds probably rest on the bottom or vegetation during incubation. Some fish remove the vegetation from the bottom; others deposit eggs on bare bottom; a few may attach eggs to vegetation.

To determine the general suitably of the ponds for the living places of fish, two determinations of the gas content of the open waters were made.

TABLE IV.

Oxygen in cubic centimeters per liter; collections 10–12 cm. below the surface of the open water.

Pond.	1	5*c*	7*a*	14*b*
July 22, 1910	6.99	4.68	7.44	6.20
April 26, 1911	6.87	7.25	6.96	6.27
Average	6.93	5.97	7.20	6.23

The table shows an oxygen content in all the ponds, sufficient to support any of the fishes.

With reference to fish breeding places, the gas content of the water was determined on four occasions. To make collections in ponds 5*c* over a sandy bottom required taking advantage of the sand areas made by artificial filling. Since there is little bare sand in ponds 7*a* and 14*b* the collections were made over the vegetation.

Table V.

Oxygen content in cubic centimeters per liter. Depth 35–40 centimeters. Sample collected at the bottom or among the upper two inches of branches of aquatic plants as indicated.

	Over Sandy Bottom.					Over Vegetation.			Bottom Materials Disturbed, Vegetation Removed in Summer				
Date.	6/27	7/22	4/26	5/10	Average.	6.27	7.22	Average.	6/27	7/22	4/26	5/10	Average.
1	6.57	6.37	5.91	6.32	6.28				3.34	5.91			4.62
5*c*	7.36	8.18	7.31	6.60	7.36				6.52	6.74			6.63
7*a*						4.42	2.52	3.47	0.00	0.00	6.26	3.36	2.40
14*b*						3.33	2.24	2.78	0.00	0.00	1.38	1.93	0.83

The table shows high oxygen content over sandy bottom, oxygen probably sufficient for most fish over vegetation, and no oxygen on the bottom where vegetation was removed in July and August.

Table VI.

Showing CO_2 Content of Water.

Depth 35–40 cm. (1) Over sandy bottom. (2) Over vegetation. (3) Over bottom with vegetation removed.

	1		5*c*		7*a*		14*b*	
	1	3	1	3	1	3	2	3
June 27, 1910	0.0	4.1	0.0	0.0	4.4	21.0	3.3	6.6
July 22, 1910	0.0	0.0	0.0	0.0	2.5	9.6	2.4	4.0
Average	0.0	2.0	0.0	0.0	3.4	15.3	2.7	5.3

The water was alkaline at points showing no CO_2. The tables do not show the uniformity that might be expected. This may be explainable on the basis of the place of collection. *Chara*, for example, which was the plant removed from the bottom of ponds 1 and 5*c*, grows on bottoms of mixed sand and humus or on a bottom covered with humus, and sufficient care was not taken in selecting places of collection, to make the differences here of importance.

There are apparently numerous factors which influence gas content (Birge and Juday, '11, p. 54). These are temperature, light as affecting photosynthesis, distance between point of collection and plants which are giving off oxygen and using CO_2, and direction and velocity of wind as affecting circulation of water. Birge and Juday (p. 55) state that European workers have noted marked diurnal changes in the amount of dissolved oxygen.

From three to four hours were required to make our collections. On June 27, the collecting began at pond 14*b* at 9:30 A.M., and ended at pond 5*c* at 12:30 P.M., temperature: pond 1, 26° C.; 5*c* and 7*a*, 27°; and 14*b*, 25°. Velocity of wind 6 miles per hour. This was a cloudy day. The sun broke through the clouds before the last collection was made. July 22 was a similar day. Collection began at pond 14*b* at 8:30 A.M., and ended at pond 7*a* at 12:00 M., temperature: pond 1, 25° C.; 5*c* and 7*a*, 26° C.; and 14*b*, 24°. During the forenoon, the sun came out several times, but exact record was not kept of the time or length of such periods of sunshine. All the other collections were made in full sunlight. Wind and temperature were as follows: April 26, temperature: 1, 13½°; 5*c*, 14½°; 7*a*, 15½°; and 14*b*, 14°; wind: 3 miles per hour. May 10, temperature, 23°; wind: 36 miles per hour. Just what effect distance from plants which were doing photosynthetic work has on gas content is not known. It is highly probable that collections made near to such plants would be different from those taken at a greater distance (Birge and Juday, '11, pp. 54 and 60).

The summer collections from pond 7*a* were taken from beneath the water lily leaves at the extreme east end where lilies have displaced the *Chara*.

Collections taken after scraping the vegetation from the bottom show various results depending upon the character of the bottom beneath the vegetation.

2. *Biological Content of the Pond.*—(*a*) Qualitative Comparison. (1) Species of Plants and their Abundance. The qualitative differences in ponds as shown in Tables VII. and VIII.

(2) Growth Form of the Plants. Pond 1 is dominated by submerged plants. There are no broad-leaved shade producers.

Table VII.

Showing the Plants of the Centers of the Ponds.

Data by Mr. G. D. Fuller. D = dominant; A = abundant; C = common; F = few.

Common Name.	Scientific Name.	Pond Numbers.			
		1	5*c*	7*a*	14*b*
Stonewort	*Nitella batrachosperma*	C	......	......	......
Stonewort	*Chara* sp. 1	D	D	C	......
Pondweed	*Potamogeton lucens* L.	C	C	F	......
Slender naias	*Naias flexilis* Rostk. & Schmidt.	C	D	F	F
Pondweed	*Potamogeton pectinatus* L.	A	?	C	F
Filamentous green algæ	....	F	F	F	A
Hornwort	*Ceratophyllum demersum* L.	A	......	F	?
Yellow water lily	*Nymphæa advena* Ait	......	F	C	F
Pondweed	*Potamogeton americanus* C. & S.	......	C	F	F
Water-milfoil	*Myriophyllum spicatum* L.	......	......	F	F
Bladderwort	*Utricularia vulgaris* L.	......	......	C	A
White water lily	*Castalia tuberosa* Greene	......	......	A	A
Water shield	*Brasenia Schreberi* Gmel.	......	......	A	C
Stonewort	*Chara* sp. 2	......	......	......	C
Bulrush	*Scirpus validus* Vahl.	......	......	......	F
Duckweed	*Lemna minor* L.	......	......	......	C

Table VIII.

Showing the Marginal Plants.

Data by Mr. G. D. Fuller.

Roots Usually Submerged.

Common Name.	Scientific Name.	Pond Numbers.			
		1	5*c*	7*a*	14*b*
Bulrush	*Scirpus validus* Vahl.	F	F	F	C
Cattail	*Typha latifolia* L.	......	......	F	C
Mermaid weed	*Proserpinaca palustris* L.	......	......	......	C
Roots Submerged at High Water.					
Sedges	....	C	F	......	......
Pines	*Pinus Banksiana* Lamb.	......	C	C	F
Shrubs (other than those below)	....	......	F	F	......
Button bush	*Cephalanthus occidentalis* L.	......	......	F	C
Willows	*Salix* spp.	......	......	F	C
Swamp white oak	*Quercus bicolor*	......	......	......	F

Pond 5*c* shows the beginning of shade producers such as the water lily and of plants which reach above the surface of the water. Pond 7*a* has a large number of emerging plants. In one end of this pond there are many more of these than in the other. In pond 14*b* emergents are dominant.

(3) Animals. The different species of animals and their ar-

TABLE IX.

LEECHES.

Name.*	Pond Numbers.				
	1	5*c*	7*a*	14	30
Glossiphonia fusca Castle	*	......	......	......	......
Erpobdella punctata Leidy	*	*	*	......	......
Dina fervida Verrill	*	*	*	*	......
Macrobdella decora Say	......	*	*	*	......
Hæmopsis grandis Verrill	......	*	*	*	......
Placobdella parasitica Say	......	......	*	*	......
Placobdella rugosa Verrill	......	......	*	*	......
Glossiphonia heteroclita	......	......	......	......	*
Hæmopsis marmoratis Moore	......	......	......	......	*

* For meaning of stars and letters see p. 11.

TABLE X.

SPHÆRIDÆ AND UNIONIDÆ.

Name.	Pond Numbers.				
	1	5*c*	7*a*	14*b*	30
UNIONIDÆ:					
Lampsilis luteolus Lam	*	......	......	......	......
Anodonta grandis Say	*	*	......	......	......
Anodonta marginata Say	*	*	*	......	......
Anodonta grandis Footiana Lea	......	*	*	......	......
SPHÆRIDÆ:					
Musculium truncatum Lins.	......	*	*	......	*
Musculium securis Prime	......	......	*	?	*
Musculium partumeium Say.	......	......	......	*	?

TABLE XI.

SNAILS.

Name.	Pond Numbers.				
	1	5*c*	7*a*	14*b*	30
Amnicola:					
Amnicola limosa Say	*	*	*	*	......
Amnicola limosa cincinnatensis Lea.	*	*	*	*	......
Amnicola limosa parva Lea	......	......	*	*	......
Physa:					
Physa gyrina Say	F	F	C	C	C
Physa heterostropha? Say (?)	......	......	......	*	......
Lymnæidæ:					
Planorbis bicarinatus Say	F	F	......	......	......
Lymnæa humilis modicella Say.	*	*	*	......	......
Lymnæa obrussa Say.	*	*	*	......	......
Planorbis albus Mul	*	*	*	*	......
Planorbis parvus Say	*	......	*	*	......
Planorbis campanulatus Say	*	*	*	*	......
Lymnæa reflexa Say.	F	F	C	A	A
Planorbis deflectus Say	......	......	*	......	......
Planorbis hirsutus Gld	......	......	......	*	*
Planorbis trivolvis Say	......	......	......	C	A
Segmentina armigera Say	......	......	......	*	?

Table XII.

Crustacea.

Name.	Pond Numbers.				
	1	5c	7a	14b	30
Hyalella Knickerbockeri Bate	C	C	C	F	F
Eucrangonyx gracilis Smith	......	F	C	A	A
Mancasellus danielsi Rich	......	......	......	......	*
Asellus communis Say	......	......	......	......	*
Cambarus immunis Hagen	F	F	C	C	C
Cambarus blandingi acutos Girard	......	......	......	F	?

Table XIII.

Aquatic Insect Larvæ and Nymphs.

Name.	Pond Numbers.				
	1	5c	7a	14b	30
May flies:					
Cœnis sp	*	*	*	*	......
Siphlurus sp	*	*	*	*	*
Callibœtis sp	......	......	......	......	*
Neuroptera:					
Chauliodes rasticornis Ram	*	*	*	*	*
Damsel flies:					
Lestes sp	*	......	......	......	......
Enallagma sp	*	?	*	*	......
Ischnura verticalis Say	......	*	?	*	*
Dragon flies:					
Tramea lacerata Hagen	*	......	......	......	......
Celithemis eponina Drury	*	......	......	......	......
Libellula pullcella Drury	*	*	......	......	......
Gomphus spicatus Selys	*	*	*	......	......
Leucorhinia intacta Hagen	*	*	*	*	......
Anax junius Drury	*	*	*	*	*
Sympetrum rubicundulum Say	......	*	......	......	......
Sympetrum sp	......	......	*	?	*
Caddice worms:					
Geora sp	*	......	......	......	......
Leptocerinœ sp	C	F	......	......	......
Neuronia sp	......	......	F	C	A
Diptera larvæ:					
Chironomid larvæ	*	*	*	*	*
Stratiomyid larvæ	*	*	*	*	*
Tanypus sp	....	*	?	*	......
Tipulid larvæ	......	......	......	*	?
Ceratopogon sp	......	......	......	......	*
Hemiptera:					
Ranatra kirkaldyi Buen	*	*	......	......	......
Corixa sp	*	*	*	......	......
Ranatra fusca P.B	*	*	*	?	?
Belostoma fluminea Say	......	*	*	*	*
Notonecta undulata Say	......	*	*	*	*
Buenoa platycnemis Fieb	......	......	F	C	?
Plea striola Fieb	......	......	......	......	*
Water striders:					
Gerris rufoscutellatus Lat	*	......	......	......	......
Gerris marginatus Say	*	?	*	......	......
Mesovelia bisignata Uhl	*	......	*	......	......

Table XIV.

Higher Vertebrates.

The fish are shown in Table XXI, page 17.

Name.	Pond Numbers.				
	1	5c	7a	14b	30
Aromochleys odorata Lat.	*	*	......	......	......
Rana pipiens Sch.	*	*	*	*	*
Chrysemys marginata Ag.	*	*	*	*	*
Malacoclemmys geogtaphica Les.	......	*	......	......	......
Diemictylus viridescens Raf.	......	*	*	*	*
Fiber zibethicus Linn.	?	?	?	?	?

The presence of the muskrat is indicated by the presence of holes, nests, tracks, etc., but none have been seen except in the oldest ponds.

rangement with respect to the ages of the ponds are shown in Tables IX. to XIV. Letters indicate relative abundance: F = few; C = common; A = abundant. The star is used to indicate presence where relative abundance has not been ascertained. For comparison, a fifth pond (No. 30) is added; this is older than the others in every respect and contains certain species of importance to fish which are not found in any of the others.

(4) Discussion of the Tables. The tables represent not only much careful collecting, but long experience with the common forms of the ponds. An inspection of the tables shows that there are differences in the species in the different ponds and that the differences are correlated with the ages of the ponds. For example, in the case of the leeches, Table IX., page 9, none of the species of the youngest pond is found in all of the ponds and none of the species of the oldest is found in the youngest. Accordingly as we pass from the youngest to the oldest we note that species disappear and are replaced by other species. The same will be seen to be true of the other groups. A similar relation is illustrated also where we have been able to estimate relative abundance. In some cases the number is greater in the older ponds; in others, less in the older ponds (*e. g.*, *Hyallela Knickerbockeri*, Table XII., page 10).

The case of the caddice worms and other aquatic insects which are placed in the water by the laying female, is of especial interest as the resulting distribution is probably either a matter of selec-

tion on the part of the female during the breeding season or striking elimination of all eggs laid in the ponds in which the larvæ are not found.

It is evident that ecological types (here represented by the various species) succeed each other as the ponds change with age. Succession is here as elsewhere, a succession of all, or at least a majority of the animals present.

(*b*) Quantitative Comparison. (1) Vegetation. Vegetation is evidently a good index of the content, or the relative numbers of the different species of plants and animals. In Table I., page 3, we note that more than two thirds of the bottom of pond 1 is covered with humus. Vegetation covers about 70 per cent. of the area. In pond 5*c* vegetation covers about 95 per cent. and in 7*a* about 99 per cent. of the area and in 14*b* 100 per cent. If the plants of each unit area were equal in volume, these percentages would represent relative volume also. More of the plants of the older ponds reach to the surface; plants are closer together in the older ponds. It is obvious from inspection that the volume per unit area is greater in the older ponds.

A single test was made with a large tow net. The net was drawn a distance of 40 feet in three of the ponds and the volume of vegetation torn off by the net was measured by displacement and reduced to terms of 100. This would give relative volume if all plants were torn with equal ease.

Finally Mr. G. D. Fuller and myself have made an estimate based on several inspections.

TABLE XV.

SHOWING MEASUREMENTS AND ESTIMATES OF RELATIVE VOLUME OF VEGETATION PER CUBIC UNIT.

Pond.	1	5*c*	7*a*	14*b*
On the basis of areas of vegetation.......	70	95	99	100
Tow net collections....................	14 c.c.	—	30 c.c.	100 c.c.
Estimate............................	20	40	60	100

(2) Plant and Animal Food. The plant and animal food in solution is expressed in a general way by the sanitary analysis. The results of a single analysis with the total carbonates added, are given in Table XVI.

Table XVI.

Showing Contamination of Pond 5*c* and Elementary Food Substances and Carbonates in All.

Single analysis, Oct. 26, 1909.

	1	5*c*	7*a*	14*b*	Wolf Lake.
Chlorine	18.4	49.7	9.9	14.2	16.3
Free ammonia	0.100	0.170	0.040	Trace	0.005
Albuminoid ammonia	0.125	0.150	0.175	0.250	0.200
Nitrites	Present	Trace	Trace	.....	Trace
Nitrates	0.160	0.030	0.030	0.040	0.060
Total carbonates	138.800	139.800	160.200	160.300	111.500

The chlorine content is regarded as a good index of the presence or absence of sewage contamination, excreta being high in chlorine compounds. 49.7 parts per million in pond 5*c* would indicate such contamination. Until very recently a house was located on the margin of pond 5*c*; the pond is still subject to contamination by domestic fowls.

Free ammonia is the final stage in the breaking down of proteids and appears also in animal excreta. It is used by plants and evidently plants consume it in proportion to their volume.

Albumenoid ammonia probably represents metaboloids in solution, because the water was filtered before determinations were made. Sewage is rich in such compounds and sanitary analysts have found that the number of bacteria is closely correlated with amount of albumenoid ammonia.

(3) Bacteria. Dr. P. G. Heinemann and Mrs. Class, of the Department of Bacteriology of the University of Chicago, very kindly made the counts of the bacteria. The results are given in Table XVII.

Table XVII.

Aerobic Bacteria per cc., Capable of Growing again at 20° C.

	1	5*c*	7*a*	14*b*	Wolf Lake.
October 26, 1909	158	48[1]	1,200	2,600	507
April 29, 1911	1,400	500	3,700	4,500	

[1] The number here does not correspond to the albumenoid ammonia, but may be partially accounted for by the fact that the bottle was accidentally opened near the surface. On April 26 a collection at the surface of the pond showed 350 (500 at bottom).

The table shows that the number of bacteria is greater in the older ponds, except in 5*c* which is noncomparable because of contamination.

(4) The Plankton. The study of the plankton has been practically limited to the Entomostraca—the most important food of young fishes. The presence of a *larger* number of rotifers and protozoa, etc., is observable as we pass from the younger to the older ponds.

The number of Entomostraca in approximately 90 liters of surface water, to a depth of 10–12 decimeters, is given in the table below. It was thought best to simply dip the desired amount from the water while walking and strain the dippings through a bolting cloth strainer. After the first collection this was repeated in as uniform a manner as possible and Birge net collections were made at the same time for comparison. There was no great discrepancy in the results of the two methods of collecting, except in the case of Ostracoda in pond 14*b*. As compared with dippings, some Birge net collections showed less Ostracoda. Ostracoda were probably started from the bottom by the feet of the collector but were not by the drawing of the Birge net.

TABLE XVIII.

THE NUMBER OF ENTOMOSTRACA IN 90 LITERS OF WATER.

	1	5*c*	7*a*	14*b*
September 3, 1909	556	...	539	2,773
November 13, 1909	200	106	397	350
March 26, 1910	42	40	12	00
May 31, 1910	3,497	1,014	4,368	3,600
July 22, 1910	160	200	520	6,480
April 26, 1911	1,250	150	140	525
May 10, 1911	100	800	125	5,125
Total of 6	5,249	2,310	5,562	16,080
Average of 6	874	385	927	2,680

The table shows that with the exception of pond 5*c*, which is probably noncomparable because of contamination, the older ponds contain most Entomostraca except in early spring when conditions are somewhat reversed.

A large quantity of plankton in old ponds has been noted for several years in connection with class work. For comparison with the ponds under consideration we have studied Wolf Lake,

and two small ponds near it. The younger of the small ponds will be designated as I. and the older one, II. They differ (with the exception of the margin vegetation) in much the same manner as do ponds 1 and *7a* of the series of special study. While Wolf Lake is not strictly comparable to the others, it is ecologically the youngest, because of its greater area of bare bottom. The collections (made Sept. 3, 1909) were four in number in Wolf Lake, four in pond I., two in pond II., one half from the open water, and one half from among vegetation. Several collections were made Apr. 30. The numbers given are the averages of all collections made on those dates. They were net collections made in as uniform a manner as possible.

TABLE XIX.

COLLECTIONS SHOWING DIFFERENCES IN NUMBERS OF ENTOMOSTRACA CORRELATED WITH DIFFERENCES IN ECOLOGICAL AGE.

Date.	Order.[1]	Body of Water.		
		Wolf Lake.	I.	II.
September 3	Copepoda	149	128	918
	Cladocera	64	96	3,936
	Ostracoda	0	8	81
	Total	213	232	4,115
April 30	Copepoda	3,750	1,500	26,600
	Cladocera	200	12,500	500
	Ostracoda	400	0	1,500
	Total	4,350	14,000	28,600

This table shows the same features as the preceding.

(5) The Larger Animals. Little has been done in estimating the relative number or volume of the larger animals in the different ponds. A general idea is given below in Table XX. This

[1]THE RELATIVE NUMBER OF THE ORDERS OF ENTOMOSTRACA IN THE COLLECTIONS OF 1910.

Order.	Pond Numbers.			
	1	5*c*	7*a*	14*b*
Copepoda	4,523	1,167	4,774	4,520
Cladocera	371	273	421	1,657
Ostracoda	25	40	202	4,673
Total	4,919	1,480	5,407	10,850

The deficiency in 5*c* is due mainly to small numbers of copepods.

is based on the general impression which has been acquired in taking classes to these and other ponds of similar character several times per year during six years. Secondly, by taking the time required to make a representative collection from the different ponds. On the basis of this experience, the figures given in the table are thought to be very conservative. That there is a far greater number of animals and a greater volume of animal substance in the old ponds is very easily demonstrated to any one by inspection.

TABLE XX.

SHOWING AN ESTIMATE OF THE RELATIVE NUMBERS OF THE CHIEF ITEMS OF FISH FOOD IN THE DIFFERENT PONDS.

	1	5*c*	7*a*	14*b*
Entomostraca	32	15	35	100
Chironomid larvæ	80?	80?	80?	100?
Sphaeridæ	0	30	50	100
Gilled snails	20	30	50	100
Pulmonate snails	10	30	50	100
Amphipods	50	70	90	100
Decapods	10	30	50	100
Insects	40	60	90	100
Fish	80	100	70	30

Previous to being drained pond 14*a* should be rated at 70 for fishes.

While the results here presented are not such as to justify conclusions concerning details, we may state that the amount of life per unit volume unquestionably increases as the ponds grow older, at least up to stages like 14*b*. Qualitative differences are shown in the Tables VII. and XIV., and the total number of species recorded in each pond is about the same, the actual quantity is far greater in the older.

III. THE CAUSES OF SUCCESSION OF FISH.

A discussion of succession must be made with reference to all the organisms of the habitat, or at least a large number of them considered in mass. Succession of one group of organisms taking place without the succession of others in the same environment seems improbable. A discussion with reference to fish must take other organisms into consideration.

1. *Statement of the Problem.*—A clear understanding of the problem at hand will perhaps be facilitated by a careful state-

ment of the question before us, after which we shall discuss the available data with reference to the relations of fish to the different ponds, from the standpoint of their area, their depth, minerals and gases in solution and finally the available food for young and adults. Competition, living place and breeding place of the fish will be discussed as fully as data will permit.

Table XXI.

Distribution of the Fish and their Relation to Bottom.

The letters and numbers at the heads of the columns refer to the various isolated parts of ponds. The star indicates the presence of the species; B, that very young specimens were found in numbers and the species bred in 1909, 10 or 11. The nomenclature and bottom preference data are after Forbes and Richardson, '08.

Common Name.	Scientific Name.	Ponds.				Bottom.	Bottom.
		1	5*c*	7*a*	14*b*	Preferred (F. & R., '08).	Present or Absent with Fish.
Large-mouthed black bass....	*Micropterus salmoides*.....	B	...	...	...	Rock and sand.	Present.
Blue gill........	*Lepomis pallidus*	B	...	...	...	Rock and sand.	"
Blue-spotted sun fish.	*Lepomis cyanellus*.....	B	...	...	...	"	"
Pumpkin seed...	*Eupomotis gibbosus*......	B	...	...	...	"	"
Warmouth Bass.	*Chænobryttus gulosus*.......	B	...	...	...	Mud.	Muck present
Yellow perch....	*Perca flavescens* .	B	B	...	...	....	....
Chub suckers...	*Erimyzon sucetta*	B	B	...	...	Rock and sand.	In part.
Spotted bullhead......	*Ameiurus nebulosus*.....	*	B	B	...	....	....
Tadpole cat.....	*Schilbeodes gyrinus*.......	*	B	B	...	Mud and sand.	In part, muck present
Pickerel........	*Esox vermiculatus*	B	B	B	...	....	....
Mud minnow...	*Umbra limi*.....	*	B	B	...	Mud (Abbott).	Muck present
Golden shiner...	*Abramis crysoleucas* ...	...	B	B	...	Mud.	"
Yellow bullhead.	*Ameiurus natalis*	...	...	*	...	"	"
Black bullhead..	*Ameiurus melas* .	...	...	B	B	"	"

The problem of the causes of succession may be stated in two ways:

(*a*) Involving interpretation: Why are the pioneer fishes of a pond succeeded as the pond grows older, by fishes of different habits?

(*b*) Independent of interpretation: Why are the fishes of pond I. not in the older ponds and the fishes of the older ponds not in pond I., when the channels between them have been open until the past few years?

2. *The Cause of Succession—Environment.*—(*a*) Area of the Ponds. A comparison of Table I., page 3, with Table XXI., page 17, and a comparison of Table I. of the preceding paper with the map (p. 131 of the preceding paper) show that most of the fishes are in ponds of all the available areas of the region, with the exception of several species which are confined to pond I., and which, on account of their numbers, could find no advantage in such close quarters. Evidently no part of the answer lies in the matter of size.

(*b*) Depth of the Ponds. A comparison of the records of depths given in Table II., page 4, with Table XXI., page 17, shows a situation parallel to the one with reference to area. Species are in ponds of various depths and are absent from ponds of depths the same as and greater than the ones in which they are found. These ponds are shallower than the waters which many of the species commonly occupy. The matter of depth does not seem to be of importance in the answer to the question.

(*c*) Minerals in Solution. The minerals in solution in the different ponds on October 26, 1909, are given in Table III.

(1) Qualitative Differences. The minerals represented in the analysis are those normal to waters inhabited by fish and probably important to fish. No zinc, lead, aluminum, silver, or copper, metals highly poisonous to fish (Marsh, '10), were found and there is no reason to expect their presence at another time of the year.[1] From the qualitative standpoint there is no reason to assign importance to minerals in solution.

(2) Quantitative Differences. The total solids given in Table III., p. 5, lie between the two extremes given by Marsh, '10, as probably not affecting fish and as "normal" for waters which are known to support fish in numbers. He gives 484 parts per million for the Potomac River and 242 for other fish waters. Nor is a very great seasonal variation to be expected, because most of the animals live through the winter and the vegetation disintegrates very slowly, especially through the cold weather,

[1] Because of the small amount of inwash, this set of ponds affords an unusual opportunity for the study of the effect of a varying amount of vegetation on the chemical composition of the water. For a statement of the salts tied up by plants see Pfeffer-Ewert, '00, page 410.

and in the spring its place is taken by new vegetation as rapidly as the decomposition of the old takes place.

From our knowledge of the composition of river water inhabited by all the fish, before and after the floods, no great importance could be assigned to minerals, even though the complexion of the analyses changed with the season. However, no positive conclusion could be drawn without careful study of the *behavior reactions* of fish to minute quantities of salt.

(*d*) Gases. The results of gas determination are given in Tables IV., V., and VI., pp. 5 and 6. Tables IV. and V. show the gas content of the open water, above the vegetation and sandy bottom, to be sufficient for fish in all the ponds. Juday and Birge, '11, p. 130, state: "König found that he could keep fish (kind not specified) in water which contained 2.95 c.c. and 1.38 c.c. of dissolved oxygen per liter without any apparent ill effects. Thörner found that a fish epidemic was caused by the absence of free oxygen. Hoppe-Seyler and Duncan state that trout which were kept from one and a half to two and a quarter hours in water having only from 0.98 to 1.71 c.c. of oxygen per liter showed marked signs of dyspnœa. Paton, in experiments on young rainbow trout, found that a fall in the amount of dissolved oxygen below one third of the normal amount, *i. e.*, below 2 c.c. per liter of water, is prejudicial and generally fatal. Some individuals however, were able to sustain life for long periods in water which contained only minimal traces of dissolved oxygen.

"Knauthe found that carp kept for an hour and twenty minutes in water which contained 1.33 c.c. of oxygen per liter, did not show any signs of dyspnœa, while others became dyspnœic in water containing from 2 c.c. to 3.1 c.c. of this gas."

Birge and Juday state also that Mackinaw trout have been taken from waters with 1 c.c. per liter. Fish diseases are said to be more prevalent in low oxygen content (Knauthe, '07). In this case there is no reason for assigning importance to the oxygen content of the open waters frequented by fish, and this factor is nearly uniform in the different ponds. The oxygen content of the bottom is of great importance and will be discussed later in connection with breeding.

(*e*) Temperature. A single set of readings taken in the late

afternoon of a warm sunny day showed less than 1 degree of difference between the different ponds and the readings were not repeated.

(*f*) Excretory Materials in Solution. Dacknowski ('06) (see Cowles, '11) found that certain unknown water soluble substances present in bog water are poisonous to plants. Colton ('08), and authors cited by him, found that the excretory products of animals are toxic to the producer, and sometimes to other organisms. This is a physiological basis for succession. Knâuthe states that the effect of fish on their environments is important, but little of definite character is known concerning it.

(*g*) Food. The food of the fishes from these ponds has not been studied, but knowledge of the food habits of the same species was acquired from the study of literature, especially the work of Forbes and Hankinson. The species found in the ponds being known, each pond was inspected with reference to the things eaten by each fish species. Forbes gives the percentage which each item constituted in the individuals which he studied.

(1) Qualitative. The method of obtaining the results consisted in adding Forbes' percentages ['80, p. 38] for the different items of food for each species found in each pond. For example, take the food of lake specimens of the perch. These were found to have eaten fish food existing in pond 1 as follows: decapods rated at 14 per cent.; unidentified fish, 50 per cent.; Acanthopteri, 8 per cent., giving a total of 72 per cent. Pond 1 contains 72 per cent. of the food of lake perch; Cyprinidae rated at 28 per cent. do not occur (see Table XXII). For the youngest individuals (under one inch) of all the species, all the ponds are qualitatively equal. Hankinson's data on Walnut Lake species show that all our ponds are about qualitatively equal for the fish which he considers.

An inspection of Table XXII, p. 21, shows that in no case are the fish *confined* to the place where their food is *qualitatively* best, in fact, as a rule, the fish are in the pond where the food is qualitatively *poorest*. The available data on the food of fishes shows that the fish eat food *available* where they live, rather than that their *distribution is due to the presence or absence of certain food species*. Excluding students of the food of animals, the idea that food determines distribution is commonly, though erroneously, held.

Table XXII.

Qualitative Expression — Value in Fish Food.

* indicates presence of the species being considered. The averages are not averages of the figures given here, but of all Forbes' items taken separately; their number is given in the last column.

Species.	Size.	Pond Numbers. 1 Per Cent.	5c Per Cent.	7a Per Cent.	14b Per Cent.	No. of Items Averaged.
Micropterus salmoides........	1–2 in.	98	100	100	100	
	2–4 in.	100	100	100	100	
	Adults.	36	42	34	21	
	Average.	*86	88	86	85	5
Lepomis pallidus...........	1–3 in.	100	100	100	100	
	Adults.	81	81	81	81	
	Adults.	60	60	80	80	
	Adults.	91	91	91	91	
	Average.	*88	88	92	92	6
Lepomis cyanellus...........	1 in.	100	100	100	100	
	1–4 in.	96	96	96	100	
	Adults.	58	71	71	58	
	Average.	*88	91	91	89	5
Eupomotis gibbosus..........	1–4 in.	100	100	100	100	
	Adults.	81	81	87	87	
	Average.	*95	95	96	96	4
Chænobryttus gulosus.........	All.	*100	100	100	100	
Perca flavescens.............	1–3 in.	100	100	100	100	
	3–4 in.	76	76	76	76	
	Adults.	72	100	92	90	
	Adults.	56	61	64	60	
	Average.	*83	*89	88	88	6
Erimyzon sucetta............	All.	*100	*100	100	100	
Ameiurus nebulosus and *melas*.	Various young.	100	100	100	100	
	Adults.	80	93	73	69	
	Average.	*90	*96	*86	*84	3
Schilbeodes gyrinus..........	Various young.	100	100	100	100	
	Adults.	66	66	78	78	
	Average.	*83	*83	*88	89	2
Esox vermiculatus...........	1¼ in.	100	100	100	100	
	Adults.	40	40	42	42	
	Average.	*70	*70	*71	71	2
Umbra limi................	Adult.	*33	*33	*33	68	
Abramis crysoleucas.........	Adult.	86	*86	*86	86	
Ameiurus natalis............	Adult.	60	64	*64	64	

(2) Quantity of Food. The quantity of food, like the quality, is one of the reasons assigned for the distribution, migration, and extinction of animals. Although my data on quantity of food in the ponds is not as good as that on quality, a comparison is presented in Table XXIV.

In the case of the young fishes, the table follows from a comparison of the tables of Forbes with our own on Entomostraca. The quantity of food for the youngest individuals of all species is practically that of the Entomostraca: Pond 1, *32;* pond 5*c*, *15;* pond 7*a*, *35;* pond 14*b*, *100*. For the adults and young from one inch to four inches in length, an estimate of the quantity of food in each pond for each species has been made by averaging the ratings of the principal articles of food given for each species by Forbes.

TABLE XXIII.

METHOD RATING PONDS. *Ameiurus natalis.*

Diet According to Forbes.	Rating in Table XX.			
	1	5*c*	7*a*	14*b*
Insects, 30 per cent.	40	60	90	100
Fish, 34 per cent.	80	100	70	30
Decapods, 17 per cent.	10	30	50	100
Average.	43	63	70	76

The ratings being only estimates, a more accurate method is unnecessary.

An inspection of Table XXIV shows that the distribution of fish is not correlated with *quantity* of the foods known to be eaten by that species of fish in other localities. The fish are frequently *found only* in the ponds where the food is *least abundant* and no fish is found where its food is most abundant. Are the fish the cause of the deficiency of their own food? To answer this question Wolf Lake and the small ponds were studied. Wolf Lake contains many more fish than any of the other bodies of water thus far mentioned, but as it is a large body we cannot compare it with the ponds. Pond I. (see p. 15), which has been artifically separated from Wolf Lake, contains few fish—*Abramis crysoleucas*, *Umbra limi*, and *Ameiurus nebulosus* are the only species and these appear not to be numerous. Pond II. contains

TABLE XXIV.

QUANTITY OF FOOD; THE RATING OF THE PONDS FOR THE DIFFERENT SPECIES.

* shows distribution of fish.

		I	5c	7a	14b
Micropterus salmoides	Young	*37	45	72	100
	Adult	*45	65	60	65
Lepomis pallidus	Young	*37	38	62	100
	Adult	*33	50	77	100
Lepomis cyanellus	Young	*30	41	60	100
	Adult	*42	62	78	82
Eupomotis gibbosus	Young	*37	45	71	100
	Adult	*37	50	73	100
Chœnobryttus gulosus	Young	*37	43	71	100
	Adult	*53	73	83	76
Perca flavescens	Young	*40	*48	71	100
	Adult	*40	*58	70	86
Erimyzon sucetta	Young	*50	*70	90	100
	Adult	*50	*70	90	100
Ameiurus nebulosus and *melas*	Adult	*32	*55	*65	*82
Schilbeodes gyrinus	Adult	*45	*65	*90	100
Esox vermiculatus	Young	*54	*61	*61	76
	Adult	*31	*42	*60	57
Umbra limi	Adult	*35	*48	*68	97
Abramis crysoleucas	Adult	20	*31	*48	96
Ameiurus natalis	Adult	43	63	*70	76

Abramis, *Umbra* and *Esox vermiculatus* all fairly abundant. It is evident that pond I. contains fewer fish per unit volume, still it has less Entomostraca. Evidently consumption by fish does not greatly affect Entomostraca.[1] The condition with respect to Entomostraca is paralleled by other elements of fish food.

(*h*) Competition of Species. On this point we have been able to secure almost no data. The golden shiner is absent from pond I. So far as the conditions are concerned, it should be present in numbers. It is an important article of diet for many of the fishes found there, which suggests that it has been eliminated by the other fishes.

3. *Relative Importance of the Breeding Activities and General Activities.*—The activities will be separated into general and breeding.

(*a*) General Activities. This will be taken up with reference to the depth of water, kind of bottom and surrounding vegetation

[1] My statement (Shelford, '10) to the effect that the amount of fish food consumed is about the same in all the ponds of our series (I., 5*c*, 7*a*, and 14*b*) was based on 14*a*, which has been drained. Table XX., page 16, shows that was incorrect.

with which the fish are commonly associated, according to the various writers cited.

Micropterus salmoides.

Vegetation of the pond weed zone (Hankinson, '07, p. 213); 3 to 25 feet—plants: *Potamogeton*, *Naias*, *Myriophyllum*, *Elodea* (Davis in Hankinson's Report).

Generally prefers still and sluggish waters (Forbes and Richardson, '08).

Lepomis pallidus.

5 to 15 feet of water, patches of *Potamogeton* and other aquatic plants (Jordan and Everman, '02).

Pond weed zone, 3 to 25 feet of water (Hankinson, '07).

Lepomis cyanellus.

Shoals where plants were abundant; bulrushes and aquatic types (Hankinson, '07).

Small streams (Forbes and Richardson, '08).

Eupomotis gibbosus.

Plant covered shoals—0 to 3 feet (Hankinson, '07).

Chænobryttus gulosus.

Shallow mud bottomed ponds or lakes (Jordan and Everman). Still water, muddy bottom, plenty of vegetation (Meek, '08).

Deep pools and quiet water (Henshall, '03).

Perca flavescens.

Chiefly an inhabitant of the pond weed zone; seldom found in less than two feet of water (Hankinson, '07).

Gregarious; moderate depths of streams and ponds (Henshall, '03).

Erimyzon sucetta.

Limited to places where vegetation was abundant (Hankinson, '07).

Ameiurus nebulosus.

Loves mud; lives in weedy ponds and rivers without current (Jordanand Everman, '02).

Fond of mud; weedy ponds and rivers without current (Forbes and Richardson, '08, p. 206).

Pond weed zone, shallow water at night (Hankinson, '07).

Schilbeodes gyrinus.

Common in dense vegetation of the shallow, almost stagnant water of bays.

Hides under stones and logs (Hay, '94).

Esox vermiculatus.

Situations with most aquatic vegetation (Jordan and Everman, '02).

Preference for quiet muddy water; weedy streams (Forbes and Richardson, '08).

Grassy streams and muddy bayous (Henshall, '03).

Umbra limi.

Never seen swimming in the open water; only where aquatic plants formed a dense growth in shallow water (Hankinson, '07).

Bury themselves in a hole in the mud scooped out with the tail; rest there at an angle of 45° with the tail down and the head barely protruding (Abbott, '70).

Mr. Dwight L. Gardner has shown by experimental studies in our laboratory that they avoid strong light.

Abramis crysoleucas.

Common in all places where there are many water plants (Hankinson, '07).

Muddiest and apparently most uninviting holes (Hay, '94).

Ameiurus natalis.

Generally frequenting the pond weed zone from which it went into shallow water at night. Young in shallow water with dense vegetation (Hankinson, '07).

Streams with muddy bottom (Forbes and Richardson, '08).

Ameiurus melas.

Small ponds with muck bottom (Jordan and Everman, '02).

A comparison of the data above with that in Table I., p. 3, and Table XXI., p. 17, shows that the large mouthed black bass, the blue gill, the warmouth, the perch and the yellow and spotted bullheads are not in water of the depth which they prefer in other localities. The other fishes are better located as to the depth of the water.

The large mouthed black bass, the blue gill, the perch, and the spotted and yellow bullheads are found chiefly in the pond weed

zone of Walnut Lake. This is characterized by plants that do not reach the surface. They are *Chara*, hornwort, bladderwort, water millfoil, water weed, slender *Naias*, pond weeds, etc. (Davis in Hankinson, '08). These same plants grow also in the bays and coves in company with the water lily and other emerging plants.

Ponds 1 and 5*c* are dominated by submerged plants. Here the perch, bass and sunfish mentioned above are associated, with the same species and the same *growth form types* as in Walnut Lake. The bullheads are found common in the ponds in which the submerged and emerging vegetation are mixed, and which contain the greatest number of *species* of the pond weed zone of Walnut Lake. It seems impossible to draw any conclusion here as to the relation of these species to either species or growth form in plants. The whole subject is one for investigation. A comparison of Tables II., p. 4, and XXI., p. 17, shows that black bass, the sunfishes and pumpkinseed are found only where a considerable area of their preferred bottom is present.

Mud and muck are evidently not distinguished in the tables of Forbes and Richardson ('08) and it is not possible to make much use of their data here for this reason. We have noted in the preceding paper that the chubsucker prefers coarse bottom materials. If muck is included with mud (Forbes and Richardson, '08) with the exception of the warmouth and chubsucker, all are well placed. The chubsucker, the mudminnow, and the golden shiner, tadpole cats and the bullheads avoid strong light, and their association with dense vegetation which results, brings them into relations with *bottoms of fine material, e. g., muck*, because they support dense vegetation (Pond, '05).

(*b*) Breeding Activities. We give below all that has been found regarding the location of nest and eggs.

Micropterus salmoides: Sterile bottom of clay, sand or gravel, fibrous roots of the parrot feather preferred to others (Titcomb, '07, p. 10 of separate, fide Stranahan); (*b*) blackened roots of waterfoil 1 to 2½ feet of water, bulrush shoals in 12 to 15 inches of water, among conspicuous growth of bulrushes, eggs on roots (Hankinson, '07, p. 214); (*c*) leaves of trees, gravel; used when artificial fibrous nest was present (Reighard, '05, p. 48); (*d*) sand,

gravel preferred, mud, clay, or surface of plants in absence of these (Henshall, '03); (*e*) gravel, clay or mud from which all foreign materials have been removed (Smith, '07, p. 247).

Lepomis pallidus: Barren shoals; bottom pure marl or marl and sand, bottom of marl or gravel; water 5 inches to 2 feet; marl bottom with bulrushes (Hankinson, '07, p. 212).

Lepomis cyanellus: Swamp loosestrife, black bottom, 1 foot of water; marl, marl and sand, also roots (Hankinson, '07, p. 210).

Eupomotis gibbosus: (*a*) Sand bottom; 1 to 2 feet of water; sand bottom; marl and sand bottom, scant bulrush growth; marl bottom, bulrush covered (Hankinson, '07); (*b*) sand and gravel bottom not infrequently on roots (Reighard in Gill, '05, p. 513); (*c*) clear water; sand and gravel bottom (Henshall, '03).

Perca flavescens: (*a*) No nest; bare sand and gravel (river), among aquatic plants (Abbott, '75); (*b*) stones, vegetation, other submerged objects or loose in water—no nest (Smith, '07, p. 252).

Ameiurus nebulosus: (*a*) Stove pipe, etc., 4–5 feet, sand, under cover, in 3–24 in. of water (rarely more than 24 in.) (Eycleshymer, '07); (*b*) gravel and aquarium bottom (Kendall, '02; Smith and Harron, '02).

Schilbeodes gyrinus: In tin can, marl bottom, 3 feet of water (Hankinson, '07).

Umbra limi: Stuck to aquatic plants (Ryder, '86).

Table XXV.

Showing the Relation of Known Breeding Habits of Fish to Conditions in the Series of Ponds.

Name of Fish.	Breeding Bottom Present with Fish.	Depth of Water Commonly Selected: in Inches.	Depth over Breeding Grounds Present with Fish: in Inches.
Micropterus salmoides	Sand.	12–30	0–18
Lepomis pallidus	Sand.	5–60	0–18
Lepomis cyanellus	Sand.	12	0–18
Eupomotis gibbosus	Sand.	12–24	0–18
Perca flavescens	Sand and vegetation.	Quite near the shore.	
Ameiurus nebulosus	Sand under cover.	3–24[1]	0–18
Umbra limi	Vegetation.		

The data on breeding habits as summarized in Table XXV. show clearly that the *distribution* of the species whose breeding

[1] Greater depth evidently rare. Apparently *usually in very* shallow water.

habits are known is *correlated with the distribution of the conditions* necessary *for breeding.*

While our tables show that there is considerable bare bottom in the pond 5*c*, there is good evidence that this is largely due to building of the road and of the Lake Shore and Mich. Southern R. R. which separated this pond from the others and from the lake and probably excluded fish since 1851. The exposures of bare sandy bottom which are due to natural causes are usually not covered with more than six inches of water.

Turning to the perch which is abundant here we note that the eggs are extruded in the open water or vegetation as well as over terrigenous bottom. Terrigenous bottom is less necessary than to the other food fishes.

Turning to the spotted bullhead we note that the nests are probably usually made in water shallower than any of the other fishes. Only one specimen has been taken from pond I.; they are numerous in pond 5*c* and 7*a*. There are some old logs and stumps and a very narrow zone of bare sand in 6 in. and less of water in these ponds. This is commonly shaded by vegetation.

In connection with oxygen content we note that it is greatest in 5*c* where the first four species of Table XXV. do not breed. However, this pond must be regarded as in a measure non-comparable because of contamination and small amount of plankton.

The low oxygen content on the muck bottoms of the older ponds, at depths used by the fishes present in pond I., and absent from these older ones, certainly is a sufficient reason for their absence, though it is not to be expected that this is the sole cause. It is apparent also that *A. nebulosus*, which is present in the older ponds, not only breeds in shallower water but also has superior means of aerating the eggs (Smith and Harron, '02).

Succession of fish then becomes succession of *breeding conditions* and *breeding mores.* While the major factors as indicated here are related to depth and bottom, there are doubtless others.

IV. General Discussion.

There is great danger of error in dealing with such complex problems when compilation is necessary and especially when the

point of view of the compiler differs from that of the original investigator. To illustrate principles and methods we have relied upon compilation far more than could otherwise be justified. Still certain facts and relations appear to be clearly indicated by this reconnaissance. These will be roughly grouped under the heads quantitative, economic and general.

1. *Quantitative.*—As has been pointed out in the body of the paper, the quantity of living material in the form of plankton, invertebrates, and vegetation increases as a pond grows ecologically older. In our data there are two exceptions to this which must be noted: First the greater number of Entomostraca in the younger ponds in early spring and the lesser number in pond 5*c* on all occasions. The greater number in the early spring is not easily explained but may be due to the better conditions on the bottom where the eggs, etc., of the plankton Entomostraca are found. Possibly the larger areas of clean bottom prevent their being buried and shut away from the effect of the sun's heat, oxygen, etc.

Pond 5*c* is, as we have indicated, probably not comparable on account of the contamination; also plankton production is measured in Crustacea and Marsh ('03) has pointed out possible errors in this method. A study of all the plankton constituents might show a different relation of 5*c*. Here, however, low plankton content is associated with little CO_2 (Birge and Juday, '11).

The rooted gross vegetation secures necessary salts from the soil and Pond ('05) pointed out that it increases plankton because the foods absorbed from the soil are added to the water when the plants decay. Our results are then in full accord with those of Pond. (See also Birge & Juday, '11, Knauthe, '07, p. 578.)

The greater number of large invertebrates appears to be generally closely related to the amount of gross vegetation. Nearly all such animals cling in vegetation and many of the species found in the older ponds use the vegetation as a means of reaching the surface for air, of avoiding strong sunlight, and as breeding places. The majority of such animals place their eggs into or upon the plants. Gross vegetation is also thickly covered with minute organisms which afford food for many animals.

It is probable that the amount of *rooted* vegetation in isolated

ponds may be taken as an index of plankton production. It appears that this must be true on the basis of the conclusions of Pond ('05) no matter what factor is of greatest importance in controlling the quantity of plankton. Johnstone ('08) pointed out that the plankton production follows Liebig's law of minimum—*i. e.*, quantity is determined by the food substance present in minimal quantity. If rooted vegetation is the controlling factor a deficiency in one food substance in the soil would show itself in the rooted vegetation and through this affect the plankton production of the pond.

The question of the general application of the principle of quantitative increase with age is important. It seems probable that in all bodies of water with small outflow organisms increase with age because, in addition to the effect of rooted vegetation, inwash continuously brings food substances which are tied up if not carried away by extensive outflow.

Experimental study of the *quantitative* problem is possible on the basis of such a set of ponds as those at the head of Lake Michigan. From such a set all the organisms can be transplanted and most of the conditions duplicated where closer control would be possible than in the natural ponds. There appears to be no difficulty in such experimental study except that it requires extensive facilities and institution or government support. Such ponds as ours and such ponds as may be constructed with them as a basis give promise of throwing more light on the factors controlling the quantity of life than do the large and complex bodies of water.

2. *Economic.*—The writer has no practical knowledge of fish culture and only the knowledge *which has been acquired by reading* some of the characteristic literature. Apparently the economic problems in fishes are concerned with questions of the preservation of fishes in natural waters, and their increase and maintenance against the removal for food, which makes them of economic importance. With these ends in view efforts have long been made mainly to increase fish by increasing food supply, to care for fish during the critical reproductive season by artificial hatching and pond culture, and to decrease enemies by destruction of objectionable fish and fish parasites. The preservation

of the fish environments has received little or no attention. Laws have been enacted to prevent the pollution of waters, but these have been enforced but rarely.

In practice the importance of the breeding season has been recognized by the culture workers but appears to have received little attention from the point of view of the preservation or cultivation of fish breeding places in the natural waters. Clark ('10) is one of the few who have emphasized breeding grounds. The main emphasis has been laid on nutrition (Knauthe, '07, Chap. IV.).

Our data indicate that the breeding interests and the feeding interests of still water food and game fishes are *distinctly antagonistic*. Birge ('10) pointed out that where the quantity of plankton is great and the fish food accordingly great, the oxygen content is low at the bottom and the water accordingly unsuited to the production of certain of the best food fishes. Knauthe (p. 579) states that a large fish productivity in a pond is commonly indicated by large amount of gross vegetation, but says also that the general statement that such ponds are always good producers of fish cannot be made. This indicates that there are other factors. He makes no mention of breeding and does not state the practice of pond owners as relating to the breeding. In standing and sluggish water, the problem of the balance between the food supply and the fish present seems relatively unimportant. Since feeding conditions of desirable food fishes grow better with time at the expense of the breeding conditions, the major problem is that of the *balance between feeding and breeding conditions*. It appears that such balance might be maintained easily if we had an adequate knowledge of the environmental relations of the fish. Definite knowledge as to spacing of nests in nature should give data as to breeding area required per capita by fish. With such knowledge at hand, together with the existing knowledge of food habits, it should not be difficult to maintain adequate breeding areas adjacent to good feeding areas within our waters both public and private.

3. *General.*—We have noted the aspects of the quantitative and economic problems which our data enable us to discuss. The remaining indications of the reconnaissance are those related to factors governing distribution and methods of study.

The study of factors governing distribution of fish and other animals has never been reduced to an adequate working basis. The problems are indeed complex, but the difficulty has arisen in part from two causes, namely, (*A*) the lack of knowledge of the activity which takes place within the narrowest limits (Shelford, '11[3]), and (*B*) lack of recognition of the important factors and features of the environment.

The conclusions of workers on distribution often seem to have been to the effect that the food relations of fishes should stand as first in importance, as factors of distribution. Hankinson ('10) states that the pond weed zone, the living and feeding place of the fish of Walnut Lake, is probably the most important habitat. Our evidence on the same species points clearly to the breeding grounds. Indeed much careful work must be done before broad generalization should follow, but it is evident that here as in birds (Merriam, '90; Adams, '08) and in the tiger beetles (Shelford, '07, '11[3]) the breeding place and the breeding activities are the most important. (Reighard, '10, and citations.) Is variation in nest building real or only apparent because we do not know the most important factors and seize upon details wholly unessential to fish? What are the laws governing the *mores of species?* Experimental work correlated with field observations can answer these questions, and it is at this point that contributions of lasting value can be made. The first step in the necessary work of raising natural history from its present state of vagary is to determine what activity takes place within narrowest limits and which is least modifiable in as many groups of animals as possible.

The second difficulty—lack of recognition of the important and unimportant in environments—is one which we have emphasized before.

The ecologist often uses vegetation as an index of conditions. There is objection to this. Investigators have seen that the same species of animals are not always associated with a given species of plant. Indeed, *species* of plants cannot often and perhaps usually be taken as an index of the environmental conditions of animals, especially in water, because *species* of plants are not necessarily an index of conditions. The physiological condition

of plants is the important thing and is commonly indicated by growth form (superficially but not finally) which is the index of internal physiological state induced by the surrounding conditions. Plant formations are the expression of the conditions of existence for the plants of a definite area. The formation is the fundamental unit of the ecology of communities and carries with it *no consideration of species whatever*. Identical or similar formations often do not have a single species in common. As we have pointed out before, species are of importance only in so far as their ecological constitutions are specific characters. It is not *species* of fish that we are to expect to be associated with species of plants, but *mores* of fish with *growth form* in plants or with plant formations. Furthermore, relations to vegetation which are of importance are to be expected primarily in connection with *breeding*.

Objection to the use of vegetation as an index of conditions, due to misapprehension, is to be expected. However, when the theoretical probabilities are understood, we have not the data in the case of fish, with which to determine whether or not *growth-form* and *mores* are associated. The subject is one for special experimental and observational investigation.

In connection with the problems of animal behavior, this point of view opens up a field wherein the rôle of the different environmental conditions in the control of behavior may be studied in nature as well as in experiment. As a background for the study of all aspects of behavior the point of view here presented seems to offer decided advantages.

Comparative study of behavior from this point of view has been impracticable because of a lack of knowledge of environments. Until we can acquire a knowledge and a nomenclature that shall be generally understood the worker must write extensive descriptions of the environment, and is likely to emphasize details which are of little importance.

The activities of an animal (behavior) are of great economic importance, they determine distribution. The relations of the *behavior problems and the distribution, the quantitative and the economic problems seem especially intimate, so that the investigation of any one from this point of view must contribute to all* as well as to

bring about a better unification and organization of biological science as a whole.

V. Summary of Tentative Conclusions.

1. The quantity of bacteria, plankton, vegetation and large animals increases as a pond grows older.

2. Terrigenous bottom and oxygen content decrease as a pond grows older.

3. The distribution and succession of fish are not determined by kind of food; kind of food eaten is determined by the availability in localities suitable in other respects.

4. Fish are not necessarily present where food is quantitatively greatest.

5. The food and game fishes here considered are closely associated with their breeding conditions to the neglect of depth of water, food, etc.

6. Low oxygen content on breeding grounds is a sufficient cause for their absence from the older ponds.

7. Conditions outside the breeding season are probably of secondary importance in the success of fish in a given locality.

8. The food interests and breeding interests of the food and game fish here considered are decidedly antagonistic. The former continually encroaches upon the latter.

9. Successful fish culture in ponds and small lakes depends upon the maintenance of balance between the breeding and feeding conditions.

10. Animal succession in ponds is due to an unused increment of excretory and decomposition materials which causes an increase in vegetation, a decrease in O_2, on the bottom and a general change in surrounding conditions, all primarily affecting *breeding*.

11. Succession of species is the result of stability of the *mores* of species concerned; when mores are flexible species do not succeed one another but continue with changes in behavior and physiological characters.

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